

Review

Pre-semantically defined temporal windows for cognitive processing

Ernst Pöppel^{1,2,3,*}

¹Human Science Center, and ²Institute of Medical Psychology, Ludwig Maximilian University Munich, 80336 Munich, Germany ³Barmanidae Center for the Study of Thinking, 20222 Munich, Center and

³Parmenides Center for the Study of Thinking, 80333 Munich, Germany

Neuronal oscillations of different frequencies are hypothesized to be basic for temporal perception; this theoretical concept provides the frame to discuss two temporal mechanisms that are thought to be essential for cognitive processing. One such mechanism operates with periods of oscillations in the range of some tens of milliseconds, and is used for complexity reduction of temporally and spatially distributed neuronal activities. Experimental evidence comes from studies on temporal-order threshold, choice reaction time, single-cell activities, evoked responses in neuronal populations or latency distributions of oculomotor responses. The other mechanism refers to pre-semantic integration in the temporal range of approximately 2–3 s. Experimental evidence comes from studies on temporal modulation of the mismatch negativity. These different observations indicate the existence of a universal process of temporal integration underlying the mental machinery. This process is believed to be basic for maintenance and change of perceptual identity. Owing to the omnipresence of this kind of temporal segmentation, it is suggested to use this process for a pragmatic definition of the states of being conscious or the 'subjective presence'.

Keywords: neuronal oscillation; subjective presence; complexity reduction; complementarity; temporal integration; consciousness

1. A CLASSICAL RESEARCH AGENDA FOR TEMPORAL PERCEPTION

The basic concepts of time and timing in psychology and cognitive neuroscience had been formulated during the sixties of the nineteenth century (Pöppel 1978, 2004). It was the biologist von Baer (1864) who came up with a notion of the moment, i.e. the longest possible time interval for an organism still to be considered as a 'time point'. When he gave his talk in 1860 at the foundation of the Russian Entomological Society in St Petersburg (printed only in 1865), he left behind the idea that a moment (a 'now') is a timeless border between past and future; from a biological point of view such a concept would be meaningless. On the contrary, von Baer stressed that different organisms, because of the different organization of their sense organs, and their brains most probably have different moments if measured with external means, namely clocks. This new concept of the moment is meant for organisms stepping out of the continuous flow of time as described by Isaac Newton in the foundation of

*Author and address for correspondence: Institute for Medical Psychology and Human Science Center, Goethestrasse 31, D-80336 Munich, Germany (ernst.poeppel@med.uni-muenchen.de). classical physics (Principia Mathematica Philosophiae Universalis): 'Absolute, true and mathematical time by itself and from its own nature flows equably without relation to anything external'. The moment, as described by von Baer, is species specific, and may have different physical durations in different animals; insects, snails, rats or humans are characterized by such different moments. What could be the 'human moment'?

An answer was given shortly after the speculation of von Baer by the physicist Mach (1865). He became interested in the discrimination of different temporal durations, and in studying differential sensitivities in the auditory modality he observed that there is no experience of 'duration' for intervals that are shorter than 40 ms. Stimuli with 40 ms duration or shorter are experienced as 'time points'. On the basis of this observation, one feels invited to interpret time points as discovered by Mach as the human moment hypothesized by von Baer. This time point can be conceived of as the 'temporal window' on a physical scale to construct primordial events that are the basic building blocks of the mental machinery of humans, and, thus, of conscious activity (Pöppel 1994, 1997*a*).

Nowadays, one and a half centuries later, after the first experimental attempts to investigate temporal perception, almost every psychological laboratory uses measures of reaction time to look into the

One contribution of 14 to a Theme Issue 'The experience of time: neural mechanisms and the interplay of emotion, cognition and embodiment'.

complexity and dynamics of cognitive processing. Chronometric analyses have become easy and unquestioned indicators for brain processes and cognitive activities. This experimental paradigm goes back to the Dutch scientist Donders (1969; original 1868), who used simple and choice reaction time to get a better understanding of the instance of decisions. His experiments started perhaps the most important success story in experimental psychology and cognitive neuroscience, but it is worth noting that the use of reaction times as indicators of the complexity of mental operations rests on the implicit hypothesis that such operations are essentially of sequential nature. This hypothesis hides the possibility that mental operations may actually be parallel, and that the experimental set-up selects from these parallel operations one activity and shifts it into a frame of sequentiality; by doing so, the experimenter might be seduced to conclude that other activities that have not been selected are, in fact, non-existent.

While von Baer, Mach and Donders were looking at the shortest or rather short temporal intervals that are typical for our mental machinery, Vierordt (1868) from Tübingen in Germany was interested in the question of how humans can reproduce the duration of longer temporal intervals that are presented to them in an experiment. He observed that short intervals are reproduced longer than the stimulus, and longer intervals are reproduced shorter than the stimulus. This observation implies that between long and short intervals there must be an interval, which is reproduced correctly; this interval is usually referred to as 'indifference interval'. The question came up whether such an indifference point is an experimental artefact, or whether it reflects a basic neuronal process that determines temporal perception. Interestingly, both answers are correct depending on the range of temporal intervals chosen in a given experiment.

If intervals to be reproduced in duration are selected between 1 s and several seconds (e.g. 5 s), one observes an indifference interval with some variability at approximately 3 s. Furthermore, reproductions up to the indifference point show a small variance whereas reproductions beyond this point show a sudden increase to much higher variance. The indifference point at this stimulus duration may reflect a specific neuronal process of high temporal stability being perhaps responsible for pre-semantic temporal integration (see below). It can, however, also be demonstrated that in other temporal regions, indifference points are observed that do not reflect a temporally stable integration process, but which are apparently created by the specific experimental conditions. As has been initially suggested in the adaptation-level theory by Helson (1964), human observers mentally construct a reference point, if they are exposed in an experimental setting to stimuli of different intensities or different durations. These reference points may correspond to the geometric mean of all stimuli presented during an experimental setting. The ecological reason for the construction of such reference points might be that stimuli with higher probability should be processed with better differential sensitivity, which is suggested

Phil. Trans. R. Soc. B (2009)

to happen closer to the reference point. Such a mechanism of temporal adaptation would imply the existence of a special temporal memory that is continuously calibrated by stimuli of different durations. Such a mnemonic system might be the basis for temporal impressions of something lasting long or short. If one, however, prevents the potential construction of such a reference point as has been done (Pöppel 1971), one can observe an indifference interval close to 3 s, but none for other ranges of stimulus durations.

This leads to the hypothesis that there might be different neuronal mechanisms for temporal perception depending on the range of intervals one has to deal with as an observer. If subjects are isolated from the natural environment for several weeks, one observes a 'free-running' circadian period that is usually longer than 24 hours. As Aschoff (1985) has shown for such experimental settings, there is a strong correlation between the time of activity of the subject (which is one phase of the circadian cycle, the time of sleep being the other one) and long-term estimation of time (such as for an hour or so), but there is no correlation between time of activity and short-term estimation of time (such as for intervals between 10 s and 2 min).

Looking at underlying mechanisms of temporal perception, one is led to an important paper by Wiener (1958), who has introduced the concept of oscillations as being fundamental for temporal organization and, thus, for certain aspects of temporal perception. From an organizational point, 'there are very considerable advantages in having the impulses of the nature of pulses of brief duration' (p. 202). With such an oscillatory mechanism, using sequential pulses synchronization of distributed events becomes possible, and Wiener uses the term 'brain clock'. That time might be stored by 'oscillatory pacemaker neurons' as has been suggested by Miall (1989). On the behavioural level, these concepts of oscillations correspond to the notion that subjective time must be segmented, an idea that has, for instance, been expressed some time ago by Stroud (1955) or Shallice (1964).

For a basic understanding of human cognition, it is crucial which concept of temporal processing is adopted. Taking for instance the visual system: is the integration of spatially distributed activities in the different regions of the visual cortex (Zeki 1978) determined pre-semantically by using temporal network properties, or is it determined by the content of what is processed? The main idea of this contribution is to stress the logistic machinery of temporal integration that is prior to 'what' is processed. A presemantic temporal network is used to process content, i.e. content itself does not create temporal integration. One has to distinguish strictly, with respect to the mental machinery, between two mechanisms, one being pre-semantic providing a temporal frame for processing and the other being responsible for the content of what is processed (Pöppel 1989). This idea of a necessary separation between functional domains is in accordance with theoretical considerations by Chen (2005) on the topological basis of perceptual organization.

2. TEMPORAL COMPLEXITY REDUCTION FOR CONTINUOUSLY PROCESSED SENSORY INFORMATION

If one analyses temporal perception it is important to realize that we cannot perceive time itself, but that we refer on the perceptual level only to events. On the basis of event perception, we may reconstruct the temporal machinery on the neurocognitive level if we take the position of an external observer. Accepting this basic hypothesis one is led to a special trajectory of reasoning to analyse temporal perception. One essential feature of perception or action is effortless availability; other than in cognitive processes such as rational conjecture we have an effortless access to images, words, smells, memories, feelings or movements. Looking at the complexity of the neuronal representation of information, the easy and effortless availability of the basic repertory of conscious phenomena is rather enigmatic. Apparently, the nervous system has developed strategies to overcome inherent problems of complexity. Where do these problems come from and how are they solved? There are several sources giving rise to complexity, uncertainty or even disarray of neuronal information, i.e. the physics of stimuli, biophysical constraints in the transduction of stimuli and their central anatomical representation.

One source of complexity or uncertainty comes from stimulus transduction that is principally different in the sense modalities such as audition or vision, taking less than 1 ms in the auditory system and more than 20 ms in the visual system. Thus, auditory and visual information arrive at different times in central structures. Things become more complicated by the fact that the transduction time in the visual modality is also flux dependent, i.e. objects in visual space with less flux require more transduction time at the receptor surface in the retina. Thus, to see an object with areas of different brightness or to see somebody talking, different temporal availabilities of local activities within the visual modality and similarly different local activities across the two involved modalities have to be overcome. If, in addition, somatosensory information has to be integrated to identify an object and to maintain its perceptual identity, the integrating systems in the brain are confronted with even more temporal challenges as the transduction time in the somatosensory system again is different (Pöppel et al. 1990). Obviously, challenges of integration for different sensory channels become even bigger on higher levels of processing (e.g. Iriki 2006).

For intersensory integration, besides biophysical problems as given by the transduction times, physical problems also have to be considered. The distance of objects that are caught by attention to be perceived is obviously never predetermined; anything can appear unexpectedly at any position in space with varying distances. Thus, the speed of sound (not of light) becomes a critical factor for the central availability of information. Approximately at a distance of 10 m, transduction time in the retina (under optimal conditions of brightness) corresponds to the time the sound requires to travel to the recipient. Up to this 'horizon of simultaneity' (Pöppel *et al.* 1990), auditory information arrives earlier in the brain; beyond this

Phil. Trans. R. Soc. B (2009)

horizon, visual information is earlier. Again, there must be some kind of mechanism in the neurocognitive machinery, which solves this problem of temporal uncertainty and unpredictability.

Besides biophysical and physical aspects, there is a further problem of complexity that is introduced by the specific architecture of our brain (Nauta & Feirtag 1986). As is suggested by neuroanatomical studies, there must be a considerable degree of divergence in the thalamocortical projections, i.e. each neuron innervating many cortical neurons (e.g. Szentágothai & Arbib 1974). This means that local information is spread out over a broad array of receptive neurons, and because of the different transmission times along the axons of these neurons, local information characterizing an object is not only distributed spatially in a network of neurons, but it is also spread out over time. The central neuronal representation is certainly not a passive mirror which correctly reflects what is going on out there in the world. Within the neuronal machinery, events or objects are ill defined and show a high degree of uncertainty both spatially and temporally.

A further aspect of complexity is introduced by the mode of functional representation that goes beyond the elementary analysis on the level of single neurons (Pöppel 1989). Experimental evidence using imaging technologies such as functional magnetic resonance imaging, magnetoencephalography or positron emission tomography indicates that each functional state is apparently characterized by a spatio-temporal pattern of distributed modular activities. Different modules in the visual modality (being, for instance, responsible for colour perception or face recognition) and similarly in the auditory modality (being, for instance, responsible for the prosody or the semantics of speech) are co-activated. Thus, not only on the cellular, but also on the modular level, the brain has to deal with integration of spatially distributed and temporally imprecise neuronal information which, however, on a lower although cortical level of processing, may be organized in a hierarchical fashion (Zeki & Moutoussis 1997).

How can this complexity be overcome? How can the uncertainty be minimized? In a radically cognitive approach (which in an epistemological sense might actually imply dualism with respect to the mind-body problem), one might argue that there is not even a question; the problems of complexity or uncertainty as indicated above are irrelevant as temporal noise (up to some tens of milliseconds) is rather small; on the basis of a situational analysis, the categorical definition of percepts follows a top-down analysis in which input problems or representational specifics such as temporal uncertainty become irrelevant. The bottom-up analysis of sensory information processing can be neglected.

Alternatively, if one is dissatisfied with such a theoretical frame to get rid of the problem of complexity, one must ask for a mechanism of how the brain might reduce complexity in a systematic way. There is, in fact, quite a lot of evidence with qualitatively different experimental paradigms that such a mechanism of complexity reduction may be at work (e.g. Pöppel 1997*a*). It is suggested that the problems mentioned above can be overcome if the nervous system uses stimulus-triggered neuronal oscillations as

derived from experiments on choice reaction time (Harter & White 1968; Pöppel 1968, 1970; Ilmberger 1986; Jokeit 1990). One period of such an oscillation is hypothesized to represent the functional basis of an elementary integration unit within which temporally and spatially distributed information is automatically related to each other and integrated into a unit. Such units or system states are insensitive to the exact temporal occurrence of input data. Thus, they are atemporal and provide integration intervals within which information is treated as co-temporal. There is plenty of experimental evidence for such systems in the time domain of some tens of milliseconds. Support comes from single-cell studies (e.g. Gardner & Costanzo 1980; Podvigin et al. 2004), from studies on neuronal populations (Galambos et al. 1981), from observations on latencies in eye movements (Frost & Pöppel 1976; Pöppel & Logothetis 1986) and from temporal-order threshold (e.g. Hirsh & Sherrick 1961). Interestingly, the concept of elementary integration units has also become quite fruitful for physical theories on time (Ruhnau 1994), stressing the interdisciplinary nature of the research in this field.

An important example supporting this conceptual notion comes from experiments with patients who have to undergo a general anaesthesia (Madler & Pöppel 1987; Schwender et al. 1994). During wakefulness, one observes an oscillatory activity with periods of 30-40 ms in the auditory evoked potential. During anaesthesia this oscillatory activity within the neuronal assemblies, which presumably reflects such internal system states is suppressed. As a result, such patients, process no sensory information at all. Most of these patients report that no time has passed at all between the beginning of the anaesthesia and the reawakening after anaesthesia. This oscillatory process, which is apparently implemented in the corticothalamic pathway, provides a formal framework for complexity reduction, and it is argued to be the neuronal basis for the creation of primordial events or the building blocks of conscious activity. Within this theoretical framework, the elementary integration units are also responsible for an effortless access of sensory information. Automatically (without necessity of any reasoning), temporal integration units of some tens of milliseconds bind spatially and temporally distributed information together. It is important to stress again that these integration units in their duration are not defined by what is processed as information, but that they are prior to any content to be processed. Temporal integration units reflect atemporal zones within which the direction of time is meaningless. To create a temporal order of successive events for our mental machinery, a mechanism of temporal integration has been developed on a lower level of temporal granularity that is characterized by atemporality, i.e. the before-after relationship of physically nonsimultaneous information is non-existent.

Strong experimental evidence on elementary processing units comes as indicated from research on temporal-order threshold (Hirsh & Sherrick 1961; Kanabus *et al.* 2002). In such experiments, subjects have to indicate in which temporal sequence stimuli have been presented, as to which ear was stimulated first. It has been shown that temporal-order threshold has approximately the same value of some tens of milliseconds for the visual, auditory and tactile modality. The correspondence of these values, in spite of qualitatively different transduction processes within these modalities, favours the hypothesis of a common central mechanism across these systems. As the indication of a temporal order requires that events have to be defined in the first place, in order to be brought into a sequence, one can conclude that this mechanism is also used to identify primordial events. The usefulness of measuring temporal-order threshold in brain-injured patients has been convincingly demonstrated by Wittmann et al. (2004). In general, it has been shown how useful experimental procedures on temporal processing can be applied for clinical populations (von Steinbüchel et al. 1999), although one has to be aware of the individual differences due to age, gender, experimental conditions or other factors (Szelag et al. 2004a; Fink et al. 2006; Szymaszek et al. 2006; Kolodziejczyk & Szelag 2008). Recent experiments using electrophysiological tools support the usefulness of temporal-order thresholds on the clinical level (Lewandowska et al. 2008). Interestingly, animal models have now been developed to successfully study temporal-order threshold (Wada et al. 2005).

A completely different domain of research, i.e. the study of eye movement control, also supports the notion of a temporally segmented information processing with successive steps of approximately 30-40 ms. If a subject initiates pursuit eye movements when a visual target starts to move, the latency of these movements show a multimodal distribution with temporal intervals between the modes of 30-40 ms (Pöppel & Logothetis 1986), similar to response histograms that have been observed for choice reaction time (Harter & White 1968; Pöppel 1968, 1970). Such multimodalities in response histograms can also be seen when saccadic eye movements are measured, although their average response time is much longer than the one for pursuit eye movements (Frost & Pöppel 1976). Thus, latency distributions of two types of eye movements and response histograms for choice reaction time show identical characteristics; in spite of the differences of average response time the modal distance in all cases is the same. This observation points to a common underlying temporal machinery, i.e. that processed information is temporally segmented into successive units of approximately 30-40 ms; these elementary processing units should not be understood as 'physical constants', but as operating ranges with some variability.

3. PRE-SEMANTIC TEMPORAL INTEGRATION IN THE RANGE OF 2–3 S

On a next level of complexity reduction, the primordial events identified on a level of higher temporal resolution are sequentially linked together. Observations made within different experimental situations provide evidence of the operative importance of a temporal integration mechanism, which may even be important for an understanding of what one usually refers to as 'consciousness'. Although these observations have been made in different contexts, a common underlying principle can be extracted in spite of some observational diversities. The 'botanizing' attitude to look for common principles in different realms of activities is guided by the conviction that if a phenomenon shows up in qualitatively different experiments or situations, a universal principle has to be suspected. In what follows, an answer shall be given to the question of what STOBCON, the 'state of being conscious' (Pöppel 1997b) could mean. The anchor point of the reasoning is that one can understand 'consciousness' only if one analyses temporal mechanisms of neuronal processes and behavioural acts. To analyse the potential meaning of STOBCON, it is necessary to analyse what traditionally has been referred to as 'subjective present'.

The subjective present as a basic temporal phenomenon has interested psychologists for more than 100 years (James 1890; Stern 1897). (In fact, one can even go back to antiquity: Augustinus in the 11th book of his confessions stresses that with respect to temporal perception under a phenomenological point of view there is only 'presence', past and future being mental constructions out of such a 'window of presence'.) We are now in a situation to indicate on an experimental basis how long such a subjective present actually lasts. This numerical answer can be derived from a number of different experiments, which all converge to a value of approximately 2-3 s. Support comes from different domains such as temporal reproduction, spontaneous speech, movement control, vision and audition, also short-term memory and even cultural artefacts in music and poetry. All these observations suggest that conscious activities are temporally segmented into intervals of a few seconds, and that this segmentation is based on an automatic (pre-semantic) integration process establishing a temporal platform for cognitive processing. It should be stressed, however, that this temporal platform does not have the typical characteristics of a physical constant with precise values, but it represents an operating range of a few seconds; in addition, one has to expect some interindividual variability for such a biological process.

What is the experimental evidence? If subjects have to reproduce the duration of either an auditory or a visual stimulus (see also above), one observes close to veridical reproductions with small temporal variance up to 2-3 s, and large errors of reproduction with a tendency for a shorter reproduction for longer intervals (e.g. Pöppel 1971). It appears as if short intervals can be kept as a unit in working memory, while longer intervals temporally disintegrate. This integrative mechanism up to a few seconds is selectively vulnerable after brain injuries (Kagerer et al. 2002). A unique insight into the temporal brain machinery has come also from experiments with autistic children (Szelag et al. 2004c). If subjects are asked to reproduce the duration of a temporal interval in the range from 1 to 5 s, they are perfectly able to do the experiment, but they have a strong tendency to reproduce each stimulus duration close to approximately 3 s (interestingly, they sometimes reproduce with twice the value of 3 s, as if an internally represented interval is replicated and finds its expression only after a second temporal platform of 3 s).

The results suggest that the experimental task triggers an 'eigen-operation' of the brain of temporal processing, which no longer can be modulated by external information. These observations in particular, and the paradigm of temporal reproduction in general, indicate the usefulness of this procedure for the evaluation of cognitive status of development and of cognitive competence in information processing, for instance, in patients with cochlear implants (Szelag *et al.* 2002, 2004*b*; Kanabus *et al.* 2004).

Temporal integration can also be studied by subjective accentuation of metronome beats. One of the founding fathers of experimental psychology, Wundt (1911), pointed out that temporal grouping of successive stimuli has a temporal limit of approximately 2.5 s. In such a metronome task, the subject imposes a subjective structure onto identical physical events (Szelag 1997). If auditory stimuli such as click sounds follow each other with an inter-stimulus interval (ISI) of, for instance, 1 s, it is easy to impose a subjective structure by giving a subjective accent to every second of the stimuli. If, however, the temporal interval between the stimuli becomes too long (for instance, 5 s), one is no longer capable to impose such a subjective temporal structure. The two sequential stimuli no longer can be united into one percept, i.e. temporal binding for temporally adjacent stimuli is no longer possible because they presumably are represented within successive windows of presence. Again, this experimental paradigm can be used to evaluate the developmental stage of children (Szelag et al. 1998).

In experiments with brain-injured patients, it could be demonstrated that the temporal integration process as studied with this metronome paradigm is selectively impaired after injuries in frontal areas of the left hemisphere (Szelag *et al.* 1997). Patients with injuries in these areas adopt a new strategy of integration by consciously counting successive events; the 'pop-up' impression of belongingness of successive tones is apparently lost in these patients and, thus, they reconstruct togetherness by abstract means. Effortless processing, a 'hallmark' of the human mental machinery, is disrupted in such patients.

A qualitatively different paradigm providing further insights into the temporal integration process comes from studies on temporal reversal of ambiguous figures (Gomez *et al.* 1995; Pöppel 1997*a*, 2006; Ilg *et al.* 2008). If one stimulus can be perceived with two perspectives (such as the Necker cube, or a vase versus two faces looking at each other, or rotating patterns reversing their apparent direction), there is an automatic shift of perceptual content after approximately 3 s. Such a perceptual shift also occurs with ambiguous auditory material, such as the phoneme sequence KU-BA-KU where one hears either KUBA or BAKU (Radilova *et al.* 1990); subjectively, one cannot prevent that after approximately 3 s, the alternative percept takes possession of conscious content.

Possibly, this regular shift between two potential interpretations of a stimulus is also supported in studies on binocular rivalry (Logothetis 1998), although the temporal variability and the rate of shift can be rather big as can particularly be observed in patients with

central injuries (Pöppel *et al.* 1978). A patient who had suffered a bilateral injury to his occipital lobe still showed binocular rivalry, but the spontaneous temporal switching did not take place with intervals of just a few seconds, but each perspective lasted some tens of seconds. This and similar observations indicate that brain injuries or functional deficiencies often result in a slowing down of central processing (e.g. Hari & Kiesilä 1996).

The spontaneous alteration rate in the two sensory modalities, i.e. vision and audition, suggests that normally after an exhaust period of 2-3 s, attentional mechanisms are elicited that open the sensory channels for new information. If the sensory stimulus remains the same, the alternative interpretation will gain control. Metaphorically speaking, every 2-3 s, the endogenously generated question arises 'what is new', and with unusual stimuli such as the ambiguous material, the temporal eigen-operations of the brain are unmasked. In fact, temporal integration controlling attention has been suspected since a long time. Already in the nineteenth century, the Austrian physician Urbantschitsch (1875) observed a temporal modulation of attention with a period of a few seconds using a rather simple experimental device. Recent research on 'inhibition of return' (IOR) gives a unique access to temporal control of attention (Bao et al. 2004; Zhou 2008). If one attends to a specific position in the visual field, and attention has to be redrawn to this position after a short interruption, reaction time is prolonged as if a return is 'inhibited'. The temporal window of such an inhibited return is, however, limited to a few seconds. In a model on IOR (Bao & Pöppel 2007), different neuronal structures have been identified, which participate in the attentional modulation for stimuli in the peripheral visual field. As subcortical structures such as the superior colliculus are involved in the processing of attention, one has to conclude that the temporal window of integration is not limited to the cortical mantle but includes structures of the midbrain.

Data in a study reported by Sams et al. (1993), where the amplitude of the mismatch negativity as a function of the ISI was investigated, support the above considerations of a rhythmic temporal segmentation. The mismatch negativity, a component of the auditory event-related potential, is elicited by a physical deviant stimulus such as frequency or intensity of a tone in a homogeneous stimulus sequence. If, during the experiment, the ISI is altered, the largest amplitude of the mismatch negativity is observed with an ISI of 3 s, i.e. shorter and longer ISIs result in smaller amplitudes of the mismatch negativity. As negativity indicates increased neuronal activity, this result suggests that the auditory channel is characterized by a higher neuronal activity in regular intervals. This modulation is endogenously determined, being a property of the neurocognitive machinery itself, and it implies that approximately every 3s the sensory channel is more sensitive than at other times for new information coming from the external or internal environment. Similarly, using a different technique, Elbert et al. (1991) validated a temporal window in this time domain electrophysiologically.

Temporal integration for intervals of 2-3 s is also seen in sensorimotor control. If a subject is requested to synchronize a regular sequence of auditory stimuli with finger taps, stimuli are anticipated with very small variance by some tens of milliseconds (Mates et al. 1994; Miyake et al. 2004; Takano & Miyake 2007). This kind of sensorimotor synchronization is, however, only possible within the operating range of a few seconds. If the next stimulus lies too far in the future (such as 5 s), it is not possible to programme an anticipatory movement that is precisely linked to stimulus occurrence; in such a case, movements become irregular and subjects prefer to react to the stimulus instead of anticipating it. This anticipatory mode of information processing has an important impact for everyday behaviour such as driving an automobile; in a hierarchical model of decision processes, Tanida & Pöppel (2006) have used the concept of pre-semantic temporal integration to better understand goal-directed behaviour.

Observations on the duration of intentional movements coming from ethological studies gave similar numerical values (Schleidt et al. 1987; Schleidt & Kien 1997). Members of different cultures including those from old ethnia (for instance, Yanomami Indians) show very similar temporal patterns for homologous movements, the preferential duration being 2-3 s. (A typical movement is shaking hands if one greets somebody; if such intentional movements are too short or too long, usually an emotional reaction is triggered indicating that the movement pattern violated an expected temporal structure.) On the basis of these human studies, Gerstner & Fazio (1995) have observed in various species of higher mammals that they also tend to segment their motor behaviour in the same temporal range as humans do. This observation suggests that we are dealing with a universal principle of temporal integration that transcends human cognition and behavioural control.

Supporting evidence for a specific temporal integration mechanism comes also from studies on memory and speech. In a classical study (Peterson & Peterson 1959), it was shown that the working platform for short-term retention is just a few seconds; only if rehearsal is allowed are we capable to store information for longer intervals. It has been a long-standing question whether one of the most basic psychophysical laws, Weber's law, also applies to temporal perception. It has been observed (Getty 1975) that it applies only for stimulus durations up to approximately 2-3 s. Thus, different temporal mechanisms are involved, if longer intervals have to be processed; this result corresponds to observations when the duration of temporal intervals have to be reproduced (see above). Experiments on the temporal structure of spontaneous speech on adults (Vollrath et al. 1992) and on children (Kowal et al. 1975) also show that spoken language is embedded in temporal windows of up to 3 s duration giving speech its rhythmic structure (Martin 1972; Kien & Kemp 1994). And even cultural artefacts follow this principle of temporal segmentation allowing rhythmic control: Musical motifs have been observed to blend nicely into a temporal window of approximately 3 s, and the same is true for poetry as the

duration of a spoken line in many languages corresponds to this duration. Possibly artists such as composers or poets have an implicit knowledge of the temporal machinery of the human brain and use the temporal platform of 2–3 s as a formal basis to express a motif or a verse (Pöppel 1988, 2006; Turner & Pöppel 1988).

Finally, with respect to temporal integration, it might be worthwhile to refer to classical studies on the time order error (Köhler 1923). If one has to compare different stimuli with respect to intensity, it has been observed that the stimulus presented second will be overestimated in its intensity if the temporal interval between the two stimuli becomes too long. Only if stimuli are presented within a temporal window of 2-3 s, veridical comparisons are possible and the problem of the time-order error can be prevented. Apparently, the two stimuli that have to be compared have to be represented 'simultaneously' within a temporal window to allow a proper comparison. Although they are represented sequentially, they are treated with virtual simultaneity within the window of 'subjective presence', thus allowing an adequate comparison, which is the basis for a choice and a decision. Goal-directed behaviour, which is necessarily based on a decision (Pöppel 2006), would be negatively influenced if a preceding comparison would be dependent on such order errors. Thus, the temporal window of a subjective presence, which allows appropriate comparisons is crucial for adequate behavioural control.

It is still an open question which neuronal mechanism might be responsible for this kind of atemporal integrations. Results obtained with the paradigm of mismatch negativity (Sams et al. 1993) can be interpreted as indicating an intrinsic temporal modulation of sensitivity in the cortical mantle, i.e. at least in the auditory modality. Low-frequency oscillations in the temporal range of 2-3 s have been suggested by Steriade et al. (1993) supporting a presemantic model of temporal integration. However, He (2003) has shown that such oscillatory processes might already be at work on the thalamic level in nonlemniscal structures. Possibly, temporal integration within this temporal domain is implemented in a thalamocortical network, which would favour the general notion that non-cortical structures are also essential for our mental machinery as has also been suggested in a model on the control of visual attention (Bao & Pöppel 2007).

4. PERCEPTUAL AND CONCEPTUAL IDENTITY: A SPECULATION ON THE PURPOSE OF PRE-SEMANTIC INTEGRATION

As the different experiments and observations referred above employ qualitatively different paradigms covering perceptual processes in audition and vision, cognitive evaluations, movement control, speech, cultural artefacts, mnemonic representation, perceptual accentuation or temporal integration, it can be concluded that temporal integration in the range of 2–3 s represents a general principle of the neurocognitive machinery. This universal integration process is automatic and pre-semantic, i.e. it is not determined by what is processed, but it creates a temporal window within which conscious activities can be implemented. Owing to the omnipresence of this phenomenon, it can also be used as a pragmatic definition of the subjective present, which is characterized by the phenomenal impression of 'nowness'. Temporal integration in the range of 2–3 s defines, however, also singular 'STOBCON' (Pöppel 1997b). Thus, this temporal window provides a logistical basis for conscious representation, a working platform for our phenomenal present.

The access to this temporal operating platform is apparently controlled by independent neuronal mechanisms as the observations on phenomena such as residual vision (also referred to as 'blindsight') after brain injury or surgical ablation in the visual cortex suggest (e.g. Pöppel et al. 1973; Weiskrantz et al. 1974). It has been observed that patients are still capable to process visual information although they report to be absolutely blind. This phenomenon can be interpreted as indicating a deficit with the entering operations into the temporal platform of conscious activity (Block 1995). If such an access mechanism to the temporal platform under normal circumstances is operative, the question arises whether the content of the separate and successive STOBCON is always of the same nature, i.e. whether the access machinery to conscious representation is just a passive bottleneck through which information has to be channelled to reach a temporal platform, or whether access mechanisms are characterized by specific selection processes. As there are, in principle, two qualitatively different contents of a STOBCON, one being experiential and the other being reflective (Pöppel 2006), it appears reasonable to assume that such access mechanisms are at the same time selection mechanisms under the control of the attentional machinery (e.g. Osaka & Osaka 2002). As these selection mechanisms remain implicit, one has to conclude that these driving force of conscious activity still are not completely understood.

The purpose for this omnipresent time window within the conceptual frame presented here is the creation of a time zone within which the identity of a percept or a thought is created and maintained, but that a new identity may enter conscious representation when the temporal window is closed. Only if temporal integration is automatic and pre-semantic, i.e. only if integration is independent of what is processed, can such a temporal platform be used for maintenance of perceptual or conceptual identity. Thus, the complementarity of identity and dynamics, which are essential for perception and thinking, is made possible by such a temporal window. Complementarity is here conceived as a generative principle: the brain creates temporal windows of just a few seconds within which the identity of a percept or a concept is maintained (stationarity), and allows after such an interval the access of a new percept or concept (dynamics). Both stationarity and dynamics are necessary for our mental machinery allowing identity and change to new identity of mental content throughout the continuity of time.

The author would like to express his gratitude to two anonymous reviewers and to Evgeny Gutyrchik, Eva Ruhnau and Marc Wittmann for critical comments. The author's research was supported by Deutsche Forschungsgemeinschaft, Bundesministerium für Bildung und Forschung, Germany, the Bavarian Government and Honda Research and Development.

REFERENCES

- Aschoff, J. 1985 On the perception of time during prolonged temporal isolation. *Hum. Neurobiol.* **4**, 41–52.
- Bao, Y. & Pöppel, E. 2007 Two spatially separated attention systems in the visual field: evidence from inhibition of return. *Cogn. Process.* 8, 37–44. (doi:10.1007/s10339-006-0151-x)
- Bao, Y., Zhou, J. & Fu, L. 2004 Aging and the time course of inhibition of return in a static environment. *Acta Neurobiol. Exp.* 64, 403–414.
- Block, N. 1995 On a confusion about a function of consciousness. Brain Behav. Sci. 18, 227-247.
- Chen, L. 2005 The topological approach to perceptual organization. *Vis. Cogn.* **12**, 553–637. (doi:10.1080/13506280444000256)
- Donders, K. 1868 [On the speed of mental processes.] Onderzoekingen gedaan in het Physiologisch Laboratorium der Utrechtsche Hoogeschool, 1868–1869, Tweede reeks, II, 92–120. [Transl. 1969 Acta Psychol. 30, 412–431. (doi:10. 1016/0001-6918(69)90065-1)]
- Elbert, T., Ulrich, R., Rockstroh, B. & Lutzenberger, W. 1991 The processing of temporal intervals reflected by CNVlike brain potentials. *Psychophysiology* **28**, 648–655. (doi:10.1111/j.1469-8986.1991.tb01009.x)
- Fink, M., Ulbrich, P., Churan, J. & Wittmann, M. 2006 Stimulus-dependent processing of temporal order. *Behav. Process.* 71, 344–352. (doi:10.1016/j.beproc.2005.12.007)
- Frost, D. & Pöppel, E. 1976 Different programming modes of human saccadic eye movements as a function of stimulus eccentricity: indications of a functional subdivision of the human visual field. *Biol. Cybern.* 23, 39–48. (doi:10.1007/ BF00344150)
- Galambos, R., Makeig, S. & Talmachoff, P. J. 1981 A 40-Hz auditory potential recorded from the human scalp. *Proc. Natl Acad. Sci. USA* 78, 2643–2647. (doi:10.1073/pnas. 78.4.2643)
- Gardner, E. P. & Costanzo, R. M. 1980 Temporal integration of multiple-point stimuli in primary somatosensory cortical receptive fields in alert monkeys. *J. Neurophysiol.* 43, 444–468.
- Gerstner, G. E. & Fazio, V. A. 1995 Evidence for a universal perceptual unit in mammals. *Ethology* **101**, 89–100.
- Getty, D. 1975 Discrimination of short temporal intervals: a comparison of two models. *Percept. Psychophys.* 18, 1–8.
- Gomez, C., Argandona, E. D., Solier, R. G., Angulo, J. C. & Vazquez, M. 1995 Timing and competition in networks representing ambiguous figures. *Brain Cogn.* 29, 103–114. (doi:10.1006/brcg.1995.1270)
- Hari, R. & Kiesilä, P. 1996 Deficit of temporal auditory processing in dyslexic adults. *Neurosci. Lett.* 205, 138–140. (doi:10.1016/0304-3940(96)12393-4)
- Harter, M. R. & White, C. T. 1968 Periodicity within reaction time distributions and electromyograms. Q. J. Exp. Psychol. 20, 157–166. (doi:10.1080/14640746 808400144)
- He, J. 2003 Slow oscillation in non-lemniscal auditory thalamus. J. Neurosci. 23, 8281-8290.
- Helson, H. 1964 *Adaptation-level theory*. New York, NY: Harper and Row.

- Hirsh, I. J. & Sherrick, C. E. 1961 Perceived order in different sense modalities. J. Exp. Psychol. 62, 423–432. (doi:10. 1037/h0045283)
- Ilg, R., Burazanis, S., Wohlschläger, A. M., Wöller, A., Wagenpfeil, S. & Mühlau, M. 2008 Stimulus frequency influences spontaneous perceptual reversals in ambiguous apparent motion. *Percept. Psychophys.* **70**, 437–442. (doi:10.3758/PP.70.3.437)
- Ilmberger, J. 1986 Auditory excitability cycles in choice reaction time and order threshold. *Naturwissenschaften* 73, 743–744. (doi:10.1007/BF00399249)
- Iriki, A. 2006 The neural origins and implications of imitation, mirror neurons and tool use. *Curr. Opin. Neurobiol.* **16**, 660–667. (doi:10.1016/j.conb.2006.10.008)
- James, W. 1890 *The principles of psychology*. New York, NY: Henry Holt.
- Jokeit, H. 1990 Analysis of periodicities in human reaction times. *Naturwissenschaften* 77, 289–291. (doi:10.1007/ BF01131228)
- Kagerer, F. A., Wittmann, M., Szelag, E. & von Steinbüchel, N. 2002 Cortical involvement in temporal reproduction: evidence for differential roles of the hemispheres. *Neuropsychologia* 40, 357–366. (doi:10.1016/S0028-3932 (01)00111-7)
- Kanabus, M., Szelag, E., Rojek, E. & Pöppel, E. 2002 Temporal order judgment for auditory and visual stimuli. *Acta Neurobiol. Exp.* 62, 263–270.
- Kanabus, M., Szelag, E., Kolodziejczyk, I. & Szuchnik, J. 2004 Reproduction of auditory and visual standards in monochannel cochlear implant users. *Acta Neurobiol. Exp.* 64, 395–402.
- Kien, J. & Kemp, A. 1994 Is speech temporally segmented? Comparison with temporal segmentation in behavior. *Brain Lang.* 46, 662–682. (doi:10.1006/brln.1994.1036)
- Köhler, W. 1923 Zur Theorie des Sukzessivvergleichs und der Zeitfehler. Psychol. Forsch. 4, 115–175. (doi:10.1007/ BF00410635)
- Kolodziejczyk, I. & Szelag, E. 2008 Auditory perception of temporal order in centenarians in comparison with young and elderly subjects. *Acta Neurobiol. Exp.* 68, 373–381.
- Kowal, S., O'Connell, D. C. & Sabin, E. J. 1975 Development of temporal patterning and vocal hesitations in spontaneous narratives. *J. Psycholinguist. Res.* 4, 195–207. (doi:10.1007/BF01066926)
- Lewandowska, M., Bekisz, A., Szymaszek, A., Wrobel, A. & Szelag, E. 2008 Towards electrophysiological correlates of auditory perception of temporal order. *Neurosci. Lett.* 437, 139–143. (doi:10.1016/j.neulet.2008.03.085)
- Logothetis, N. K. 1998 Single units and conscious vision. *Phil. Trans. R. Soc. Lond. B* **353**, 1801–1818. (doi:10. 1098/rstb.1998.0333)
- Mach, E. 1865 Untersuchungen über den Zeitsinn des Ohres Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften. 51, II. Abteilung. 133–150.
- Madler, C. & Pöppel, E. 1987 Auditory evoked potentials indicate the loss of neuronal oscillations during general anaesthesia. *Naturwissenschaften* 74, 42–43. (doi:10.1007/ BF00367044)
- Martin, J. G. 1972 Rhythmic (hierarchical) versus serial structure in speech and other behavior. *Psychol. Rev.* 79, 487–509. (doi:10.1037/h0033467)
- Mates, J., Müller, U., Radil, T. & Pöppel, E. 1994 Temporal integration in sensorimotor synchronization. J. Cogn. Neurosci. 6, 332–340. (doi:10.1162/jocn.1994.6.4.332)
- Miall, C. 1989 The storage of time intervals using oscillating neurons. *Neural Comput.* 1, 359–371. (doi:10.1162/neco. 1989.1.3.359)

- Miyake, Y., Onishi, Y. & Pöppel, E. 2004 Two types of anticipation in synchronization tapping. *Acta Neurobiol. Exp.* **64**, 415–426.
- Nauta, W. J. H. & Feirtag, M. 1986 Fundamental neuroanatomy. New York, NY: Freeman & Co.
- Osaka, N. & Osaka, M. 2002 Individual differences in working memory during reading with and without parafoveal information: a moving-window study. Am. J. Psychol. 115, 501–513. (doi:10.2307/1423525)
- Peterson, L. B. & Peterson, M. J. 1959 Short-term retention of individual items. *J. Exp. Psychol.* 58, 193–198. (doi:10. 1037/h0049234)
- Podvigin, N. F., Bagaeva, T. V., Boykova, E. V., Zargarov, A. A., Podvigina, D. N. & Pöppel, E. 2004 Three bands of oscillatory activity in the lateral geniculate nucleus of the cat visual system. *Neurosci. Lett.* **361**, 83–85. (doi:10.1016/ j.nevlet.2004.01.003)
- Pöppel, E. 1968 Oszillatorische Komponenten in Reaktionszeiten. Naturwissenschaften 55, 449–450. (doi:10.1007/ BF00602678)
- Pöppel, E. 1970 Excitability cycles in central intermittency. *Psychol. Forsch.* 34, 1–9. (doi:10.1007/BF00422860)
- Pöppel, E. 1971 Oscillations as possible basis for time perception. Stud. Gen. 24, 85–107.
- Pöppel, E. 1978 Time perception In Handbook of sensory physiology vol. VIII (eds R. Held, H. W. Leibowitz & H.-L. Teuber) Perception, pp. 713–729. Berlin, Germany: Springer
- Pöppel, E. 1988 The measurement of music and the cerebral clock: a new theory. *Leonardo* 22, 83–89. (doi:10.2307/ 1575145)
- Pöppel, E. 1989 Taxonomy of the subjective: an evolutionary perspective. In *Neuropsychology of visual perception* (ed. J. W. Brown), pp. 219–232. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Pöppel, E. 1994 Temporal mechanisms in perception. Int. Rev. Neurobiol. 37, 185–202. (doi:10.1016/S0074-7742 (08)60246-9)
- Pöppel, E. 1997a A hierarchical model of temporal perception. *Trends Cogn. Sci.* 1, 56–61. (doi:10.1016/ S1364-6613(97)01008-5)
- Pöppel, E. 1997b Consciousness versus states of being conscious. *Behav. Brain Sci.* 20, 155–156. (doi:10.1017/ S0140525X97300053)
- Pöppel, E. 2004 Lost in time: a historical frame, elementary processing units and the 3-second-window. *Acta Neurobiol. Exp.* 64, 295–301.
- Pöppel, E. 2006 Der Rahmen. Ein Blick des Gehirns auf unser Ich. München, Germany: Hanser-Verlag.
- Pöppel, E. & Logothetis, N. 1986 Neuronal oscillations in the human brain. Discontinuous initiations of pursuit eye movements indicate a 30-Hz temporal framework for visual information processing. *Naturwissenschaften* 73, 267–268. (doi:10.1007/BF00367781)
- Pöppel, E., Held, R. & Frost, D. 1973 Residual visual function after brain wounds involving the central visual pathways in man. *Nature* 243, 295–296. (doi:10.1038/ 243295a0)
- Pöppel, E., Brinkmann, R., von Cramon, D. & Singer, W. 1978 Association and dissociation of visual functions in a case of bilateral occipital lobe infarction. *Arch. Psychiatr. Nervenkr.* 225, 1–21. (doi:10.1007/BF00 367348)
- Pöppel, E., Schill, K. & von Steinbüchel, N. 1990 Sensory integration within temporally neutral system states: a hypothesis. *Naturwissenschaften* 77, 89–91. (doi:10. 1007/BF01131783)
- Radilova, J., Pöppel, E. & Ilmberger, J. 1990 Auditory reversal timing. Act. Nerv. Super. 32, 137–138. (doi:10. 1016/0167-8760(91)90282-3)

- Ruhnau, E. 1994 The now—the missing link between matter and mind. In *Now, time and quantum mechanics* (eds M. Bitbol & E. Ruhnau), pp. 101–130. Gif-sur-Yvette, France: Editions Frontieres.
- Sams, M., Hari, R., Rif, J. & Knuutila, J. 1993 The human auditory sensory memory trace persists about 10 sec: neuromagnetic evidence. *J. Cogn. Neurosci.* 5, 363–370. (doi:10.1162/jocn.1993.5.3.363)
- Schleidt, M. & Kien, J. 1997 Segmentation in behavior and what it can tell us about brain function. *Hum. Nat.* 8, 77–111. (doi:10.1007/s12110-997-1005-7)
- Schleidt, M., Eibl-Eibesfeldt, I. & Pöppel, E. 1987 A universal constant in temporal segmentation of human short-term behaviour. *Naturwissenschaften* 74, 289–290. (doi:10.1007/BF00366417)
- Schwender, D., Madler, C., Klasing, S., Peter, K. & Pöppel, E. 1994 Anesthetic control of 40-Hz brain activity and implicit memory. *Conscious. Cogn.* 3, 129–147. (doi:10. 1006/ccog.1994.1009)
- Shallice, T. 1964 The detection of change and the perceptual moment hypothesis. *Br. J. Stat. Psychol.* 17, 113–135.
- Steriade, M., Amzica, F. & Nunez, A. 1993 Cholinergic and noradrenergic modulation of the slow (0.3 Hz) oscillation in neocortical cells. *J. Neurophysiol.* 70, 1384–1400.
- Stern, L. W. 1897 Psychische Präsenzzeit. Zeitschrift für Psychologie und Physiologie der Sinnesorgane 13, 325–349.
- Stroud, J. M. 1955 The fine structure of psychological time. In *Information theory in psychology* (ed. H. Quastler), pp. 174–205. Glencoe, IL: Free Press.
- Szelag, E. 1997 Temporal integration of the brain as studied with the metronome paradigm. In *Time, temporality, now* (eds H. Atmanspacher & E. Ruhnau), pp. 107–120. Berlin, Germany: Springer.
- Szelag, E., von Steinbüchel, N. & Pöppel, E. 1997 Temporal processing disorders in patients with Broca's aphasia. *Neurosci. Lett.* 235, 33–36. (doi:10.1016/S0304-3940 (97)00703-9)
- Szelag, E., Kowalska, J., Rymarczyk, K. & Pöppel, E. 1998 Temporal integration in a subjective accentuation task as a function of child cognitive development. *Neurosci. Lett.* 257, 69–72. (doi:10.1016/S0304-3940(98)00809-X)
- Szelag, E., Kowalska, J., Rymarczyk, K. & Pöppel, E. 2002 Duration processing in children as determined by time reproduction: implications for a few seconds temporal window. *Acta Psychol.* **110**, 1–19. (doi:10.1016/S0001-6918(01)00067-1)
- Szelag, E., Kanabus, M., Kolodziejczyk, I., Kowalska, J. & Szuchnik, J. 2004a Individual differences in temporal information processing in humans. *Acta Neurobiol. Exp.* 64, 349–366.
- Szelag, E., Kolodziejczyk, I., Kanabus, M., Szuchnik, J. & Senderski, A. 2004b Deficits of non-verbal auditory perception in postlingually deaf humans using cochlear implants. *Neurosci. Lett.* 355, 49–52. (doi:10.1016/ j.neulet.2003.10.025)
- Szelag, E., Kowalska, J., Galkowski, T. & Pöppel, E. 2004c Temporal processing deficits in high-functioning children with autism. Br. J. Psychol. 95, 269–282. (doi:10.1348/ 0007126041528167)
- Szentágothai, J. & Arbib, M. A. 1974 Conceptual models of neural organization. *Neurosci. Res. Prog. Bull.* 12, 307–510.
- Szymaszek, A., Szelag, E. & Sliwowska, M. 2006 Auditory perception of temporal order in humans: tue effect of age, gender, listener practice and stimulus presentation mode. *Neurosci. Lett.* 403, 190–194. (doi:10.1016/j.neulet.2006. 04.062)

- Takano, K. & Miyake, Y. 2007 Two types of phase correction mechanism involved in synchronized tapping. *Neurosci. Lett.* 417, 196–200. (doi:10.1016/j.neulet.2007. 02.044)
- Tanida, K. & Pöppel, E. 2006 A hierarchical model of operational anticipation windows in driving an automobile. *Cogn. Process.* 7, 275–287. (doi:10.1007/s10339-006-0152-9)
- Turner, F. & Pöppel, E. 1988 Metered poetry, the brain, and time. In *Beauty and the brain. Biological aspects of aesthetics* (eds I. Rentschler, B. Herzberger & D. Epstein), pp. 71–90. Basel, Switzerland: Birkhäuser.
- Urbantschitsch, V. 1875 Über eine Eigenthümlichkeit der Schallempfindungen geringster Intensität. *Centralblatt für die mediz. Wissenschaften* **13**, 625–628.
- Vierordt, K. 1868 Der Zeitsinn nach Versuchen. Tübingen, Germany: Laupp.
- Vollrath, M., Kazenwadel, J. & Krüger, H.-P. 1992 A universal constant in temporal segmentation of human speech. *Naturwissenschaften* **79**, 479–480. (doi:10.1007/ BF01139205)
- von Baer, K. E. 1864 Welche Auffassung der lebenden Natur ist die richtige? Und wie ist diese Auffassung auf die Entomologie anzuwenden? In Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts (ed. H. Schmitzdorff), pp. 237–284. St Petersburg, Russia: Verlag der kaiserlichen Hofbuchhandlung.

- von Steinbüchel, N., Wittmann, M. & Szelag, E. 1999 Temporal constraints of perceiving, generating, and integrating information: clinical indications. *Restor. Neurol. Neurosci.* 14, 167–182.
- Wada, M., Moizumi, S. & Kitazawa, S. 2005 Temporal order judgment in mice. *Behav. Brain Res.* 157, 167–175. (doi:10.1016/j.bbr.2004.06.026)
- Weiskrantz, L., Warrington, E. K., Sanders, M. D. & Marshall, J. 1974 Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain* 97, 709–728. (doi:10.1093/brain/97.1.709)
- Wiener, N. 1958 Time and the science of organization. *Scientia* **93**, 199–205.
- Wittmann, M., Burtscher, A., Fries, W. & von Steinbüchel, N. 2004 Effects of brain lesion size and location on temporalorder judgment. *NeuroReport* 15, 2401–2405. (doi:10. 1097/00001756-200410250-00020)
- Wundt, W. 1911 *Einführung in die Psychologie*. Leipzig, Germany: Voigtländer.
- Zeki, S. 1978 Functional specialization in the visual cortex of the monkey. *Nature* 274, 423–428.
- Zeki, S. & Moutoussis, K. 1997 Temporal hierarchy of the visual perceptive systems in the Mondrian world. *Proc. R. Soc. Lond. B* 264, 1415–1419. (doi:10.1098/rspb. 1997.0197)
- Zhou, B. 2008 Disentangling perceptual and motor components in inhibition of return. *Cogn. Process.* 9, 175–187. (doi:10.1007/s10339-008-0207-1)